Survivorship, Growth and Behavior of Juvenile Lobsters Homarus americanus Milne-Edwards in Controlled Environments in Nature

by

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Manuscript and Technical Report Series

Project Report No. 83-02

Nova Scotia
Department of Fisheries

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May, 1983

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ABSTRACT

Field studies showed that hatchery reared stage IV lobsters survived best on rock substrate followed by vegetation followed by mud. Density did not measurably affect the survivorship of these small juvenile lobsters. No major differences in lobster growth were found among substrates but animals held in conditions of high density grew less than those in low density treatments. Extreme variations in individual growth rates were observed. Stage IV lobsters planted in underwater enclosures spent their entire time below the substrate in burrows constructed adjacent to solid structures. The activity of juvenile lobsters ceased when the water cooled in winter and resumed when temperatures increased in spring. Highest survivorship is expected on ocean bottom which enables settling larval lobsters to quickly get undercover out of the reach of predators such as crabs, eels and other fishes.

ACKNOWLEDGEMENTS

The original manuscript reporting on this research was presented by the author to Dalhousie University as a M.Sc. thesis. The work was supported in full by the Nova Scotia Department of Fisheries. Hatchery facilities were provided by Dalhousie University. Split train rails were donated by DEVCO.

I would like to thank Andrew Bagnall, Barry Smith, Jack Finlayson and all the summer students who participated in field activities and hatchery work. Mrs. Nina Pepper's assistance in the preparation of this manuscript was greatly appreciated.

Special thanks to the people in Isle Madame, Cape Breton who showed tremendous hospitality and assisted our field team in many ways during the course of the research.

I would like to thank Dr. Ian McLaren for his support and advice and Drs. Les Haley and Robert O'Dor for their efforts in reviewing this paper.

INTRODUCTION

The American lobster, Homarus americanus, is found along the east coast of North America from Labrador to South Carolina at depths ranging from less than 1 m to over 700 m (Herrick, 1911; Cooper and Uzmann, 1971; Wilder, 1973). This species, which supports an extremely valuable commercial fishery, has been extensively studied for the past century. Irrespective of these efforts, major gaps in our understanding of its biology still exist. The ecology of juveniles, on which this study is focusing, is one area where virtually no information is available. At present the growth rates, survivorship, behavior and even whereabouts of the early benthic stages of the lobster are unknown.

Adult female lobsters mate soon after molting (Atema et al., 1979; Aiken and Waddy, 1980) with mating and oviposition being independent. The female is capable of retaining sperm and successfully extruding eggs as soon as one month or as much as two years after copulation (Aiken and Waddy, 1980). Eggs are carried for approximately eleven months (Herrick, 1911; Templeman, 1936) and upon hatching, rapid movement of the female's pleopods frees prelarvae from the inner egg membrane. Ecdysis occurs either immediately or after a short period, and the first larval stage swims free (Davis, 1964; Ennis, 1975a). Larval release is most frequent after dark but may occur any time throughout the day (Tamm and Cobb, 1976). A complete hatch can take from 3-4 days to several weeks, depending on water temperature (Hughes and

Matthiessen, 1962; Ennis, 1975a).

In the plankton, larvae pass through four morphologically distinct stages (Herrick, 1911), the last being capable of benthic existence. Molt frequency of the larvae is effected by many environmental and physiological factors, with temperature seemingly the most significant regulator. Time to stage IV can range from 11 days at 22°C to 54 days at 10°C (Aiken, 1980). Homarus larvae are capable of swimming by beating their exopodites or they may move by rapid tail flexes (Neil et al., 1976). While in the plankton, they are subjected to surface currents and may drift far from their point of origin (Scarratt, 1964).

Young H. americanus larvae are positively phototactic (Hadley, 1908; Herrick, 1911) and in the wild are concentrated in the surface layers during daylight hours (Scarratt, 1973). During stage IV larvae become strongly photonegative (Hadley, 1908; Scarratt, 1973; Botero, 1980). Larvae also respond to changes in hydrostatic pressure and it is suspected that a combination of light and pressure mechanisms regulate depth orientation (Ennis, 1975b).

Homarus larvae settle to the bottom during stage IV (Herrick, 1911; Scarratt, 1964; Berrill, 1974; Botero, 1980) and remain there for the rest of their lives. Successful location and establishment in an appropriate substrate is essential for survivorship. Gray (1974) and Crisp (1974) report that settlement of benthic organisms appears to be far from random. Larvae of many different species respond to

specific environmental cues and time spent in the plankton may be governed by the ability to locate the correct substratum. Cobb (1968) and Botero (1980) observed that stage IV lobsters delayed their molt to stage V in the absence of a preferred substrate.

Adult lobsters are known to occupy habitats characterized by sand/rock, bedrock/rock, mud/silt and mud/rock, the most common being a sand substrate with overhanging boulders and rocks (Cooper and Uzmann, 1980). They are also found on ocean bottom covered by marine macrophytes (Mann & Breen, 1972; Scarratt, 1971). Young benthic juveniles, however, are extremely difficult to locate and for years have been eluding researchers attempting to sample them quantitatively by scuba diving or trapping (Howard and Bennett, 1979). Early reports by Herrick (1911) and MacKay (1929) state that very small lobsters can be found in shallow water under rocks or in small tunnels on muddy bottom. Cooper and Uzmann (1977) found concentrations of stage IV to X animals inhabiting tiny burrows constructed in mud substrate. Laboratory studies by Berrill and Stewart (1973), Berrill (1974) and Botero (1980) indicate that young juvenile Homarus are well adapted for living on a mud substrate and will dig and inhabit tunnels if the mud is firm enough not to collapse. Tunnels were often U-shaped (Howard and Bennett, 1979) with two openings on the mud surface, and similar to those described by Rice and Chapman (1971) for Nephrops norvegicus.

Although adapted to living in mud, juvenile lobsters will often select other substrates when given a choice.

Botero (1980) found that stage IV larvae preferred a sand bottom overlaid with seaweed-covered rocks, followed by mud, followed by gravel, followed by flat sand. Studies of stage VII to X juveniles demonstrated their preference for substrate of small rocks over mud or silt (Pottle and Elner, 1982; Howard and Bennett, 1979). Howard and Bennett (1979) report that juvenile lobsters have wide habitat tolerances enabling them to inhabit a variety of substrate types. No information is available on the advantages of any particular substrate nor are there data on the type of ocean bottom which would enable the highest survivorship for young juvenile lobsters.

Lobsters grow by molting with growth rates dependent on the molt frequency and the size increment. In studying the European lobster Homarus vulgarus, which is closely related to H. americanus, Hewett (1974) noted that with an adequate food supply the growth increment is a constant proportion of the lobster's weight and variations in growth rate are due to changes in the length of the intermolt period which in turn is mainly dependent on temperature. Hughes and Matthiessen (1962) found that molting activity for American lobsters peaked in the 15-20^{o}C temperature range while Aiken (1980) reports that molt induction ceases at approximately 5^{o}C.

Conditions which forced a high degree of crowding between adult male lobsters resulted in greatly reduced molting frequencies (Stewart, 1968). Cobb (1970) found that one member of a pair of stage IV lobsters held together would show a delay in molting. Cobb and Tamm (1974) found that paired stage XI juveniles prolonged intermolt periods by an

average of 25-30% and a delay in mean time to molt of as high as 70% was observed for the second animal. The same researchers (Cobb and Tamm, 1975) reported that the dominant juvenile of a pair would be the first to molt.

The size increase at ecdysis is relatively greater and the intermolt period shorter in younger lobsters (Templeman, 1940; Wilder, 1953; Mauchline, 1977). Growth equations and size estimates at age have been developed for American lobsters (Wilder, 1953: Thomas, 1973; Mauchline, 1977; Cooper and Uzmann, 1977) but no reliable technique exists to age a lobster. A great deal of uncertainty exists about growth rates in the wild and especially lacking is information on stage IV to X juveniles.

Cooper and Uzmann (1980) described the nocturnal activity of the American lobster of the inshore population along the U.S. coastline. They noted that in summer 10% of the lobsters left their shelters during the first hour after sunset and by the fourth to fifth hour of darkness 80-90% were moving about. Nocturnal activity is inhibited by cold water and in winter active foraging is minimal.

Juvenile lobsters less than 35 mm in carapace length were not observed out of their shelter or tunnel system (Cooper and Uzmann, 1977). When individuals reached 35-40 mm in carapace length they became partially active at night, moving back and forth within the entrance of their shelter. Pottle and Elner (1982) with lab studies found that stage VII to X juveniles were active primarily but not exclusively at night. Zeitlin-Hale and Sastry (1978) found that social

conditions can affect activity levels in juveniles. They noted that the presence of conspecifics inhibited locomotor activity and that animals held without shelters displayed higher daily activity levels.

At present there are many unknowns about the ecology of juvenile lobsters in the wild. It is impossible to predict recruitment into the fishery due to problems in finding and assessing juvenile populations. Scarratt (1973) was able to correlate parent stock with stage I larval production but in other work (1964) he found no relationship between the abundance of stage IV larvae and the lobster stock developing from them. It is not until lobsters approach legal fishing size that they show up in sufficient numbers to allow estimations of the strength of a particular size group.

Larval lobsters are subjected to high mortalities during planktonic stages while natural predatory pressures on adults are minimal. It is expected that the transitionary stage from plankton to benthos is a critical one for the lobster. Time spent finding cover and protection offered by the substrate will greatly affect survivorship. The purpose of this work is to gather information on survivorship, growth and behavior of hatchery-reared stage IV lobsters planted under controlled conditions in the wild.

Tray experiments have been designed to compare the effects of different substrates, densities and predators on survivorship and growth of stage IV juveniles. Corral experiments have been conducted to observe burrowing behavior, nocturnal activity and overwinter activity of young juvenile lobsters.

Materials and Methods

Capture and rearing of larvae

In late summer of 1979 coastal areas of Chedabucto Bay were surveyed to locate a suitable research site. Lennox Passage between Isle Madame and the River Bourgeois area of Cape Breton was chosen. D'Escousse Harbour in Isle Madame was established as the base (Fig. 1).

In the spring of 1980 berried female lobsters carrying well-developed eyed eggs were obtained from an offshore fishing vessel conducting operations off Southwestern Nova Scotia. The captured animals were packed in seaweed and transported to a lobster hatchery established at Dalhousie University in Halifax. Upon arrival they were placed in large holding tanks serviced with running ambient seawater. Females chosen for a hatch were placed in an acclimation lab where water temperature was increased $3^{o}C$ per day to a maximum of $20^{o}C$. This temperature was maintained throughout egg development and larval rearing phases.

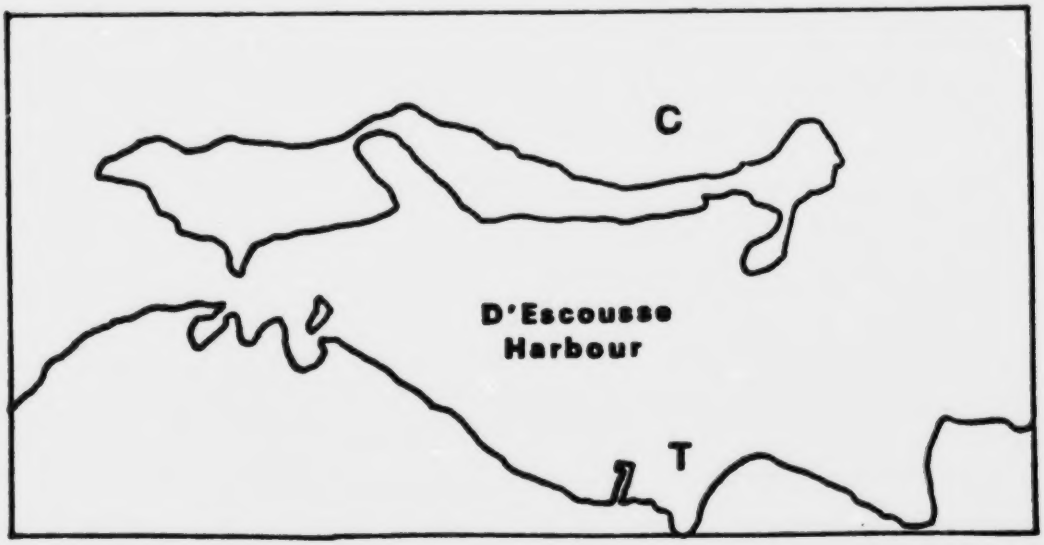
Upon hatching, stage I lobsters were collected and placed in larval-rearing tanks as described by Hughes (1974). Larvae were fed frozen adult brine shrimp Artemia salina twice daily. Concentrations of approximately three prey animals per larval lobster were maintained in the tanks.

Three to six days after reaching stage IV, the larvae were packed in plastic bags containing 2-3 liters of sea water. The bags were iced and transported in coolers to the field site in D'Escousse where the larval lobsters were

Figure 1: Experimental lobster research site in Lennox Passage, Nova Scotia. The area where trays were set is marked "T" and the location of the rock-gravel corral is marked "C".

Nova Scotia

Isle
Madame


C
D'Escousse
Harbour
T

placed in a recovery tank serviced with running ambient sea water. Only those lobsters that appeared healthy after a 18-48 hour period were used in experiments. A sample of 25 lobsters was weighed and measured to get an estimate of the average size of the animals transported. Essentially the same procedures were used for the capture of berried females and rearing of larvae in 1981 and 1982.

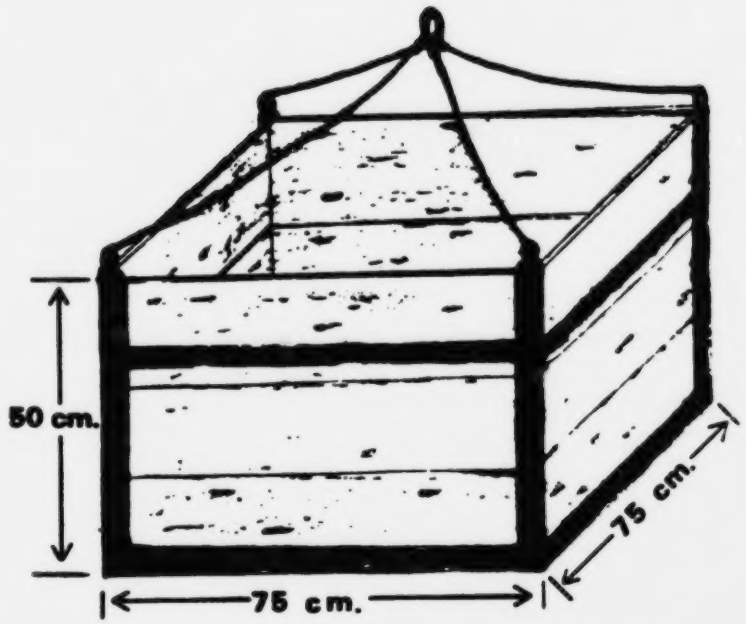
Tray Testing

Wooden trays of dimensions 75 cm x 75 cm x 45 cm were constructed and framed with angle iron (Fig. 2). Metal shackles or ropes were attached to the tops of the frames to facilitate lifting and lowering. A 2.75 m x 4.25 m raft floated by twelve 45 gallon drums was built to service the trays.

Each tray was filled with one of three substrates and designated as rock, mud or vegetation. Rocks of various sizes ranging from 2-8 cm diameter were collected from the intertidal zone and placed in submersed trays. Bulk volumes of rock were constant in all trays of this group. Mud trays were filled by scooping benthic mud into units that were placed on the bottom of D'Escousse Harbour. Vegetation trays were filled with an estimated 8 cm layer of rocks topped by a number of small boulders with attached rockweed plants Fucus spp. collected from the subtidal region.

After a substrate settling period of at least one week, trays were lifted and larval lobsters were introduced. The trays were then covered with fine-mesh nylon mosquito screen, labelled, and small cork buoys were enclosed in each

Figure 2: Experimental tray showing the metal frame and attached bridle.


50 cm.
75 cm.
75 cm.

to float the screen above the substrate. These experimental units were placed on the bottom at a depth of approximately 2 m at low tide, and remained there for two, four or six weeks.

Four densities were tested in each of three substrates. Low-density treatments were identified as those with initial numbers of 10 or 25 larval lobsters, while high-density treatments had initial numbers of 50 and 100 animals.

Scuba divers periodically serviced the trays, cleaning fouling organisms and sediments from the screen covers. Bottom temperatures were taken regularly and observations were made by peering through the screens. At the end of the designated set period trays were lifted at high tide and towed to shore. At low tide the beached trays were uncovered and sorted.

Rocks were removed singly by hand from trays containing rock substrate. Lobsters and other organisms were collected and placed in sea water as they were encountered. When all rocks were removed from a tray, its interior was washed and wash water was filtered through a screen. The tray linings were removed, washed and inspected.

The substrate surface in each mud tray was carefully inspected and visible lobsters and other animals were removed. Mud was then scooped out in successive, independently sorted layers 5-7 cm thick. A muddy mixture was made by diluting with sea water; this blend was filtered and washed and the remaining particles were sorted by hand.

Rocks with attached seaweeds were removed from the vegetation trays and plants were clipped from the rocks at the holdfasts. Plant sections were washed and carefully

inspected for any entangled animals. The remaining substrates in the vegetation trays were sorted using techniques developed for the rock treatments.

Lobsters were counted and the total length of each animal was measured to the nearest mm using Vernier calipers. The lobsters retrieved from each tray were weighed as a group to the nearest 0.1 g using a balance scale. Other species found in the trays were identified and measured. All animals were liberated after analysis.

Survivorship and growth tests were repeated in 1981 using rock, mud and vegetation substrates, two, four and six week time periods, and densities of 25 and 100. Rock and vegetation trays were covered with nylon screen immediately after substrates were added. Screens were removed to enable introduction of lobsters and replaced before setting on the ocean bottom. Mud trays were visually inspected by divers before lobsters were added and covers put in place.

Predator trials were incorporated into the 1981 tray work. Three substrates, rock, mud and vegetation, were used, twenty-five lobsters were introduced into each tray and a set period of four weeks was chosen. Two rock crabs, Cancer irroratus, or two starfish, Asterias vulgaris, were added to the predator trays. No suspected predators were added to control trays.

Sorting techniques for all trays were similar to those described for the 1980 work. Total lengths of retrieved lobsters were measured to the nearest mm. Group weights of

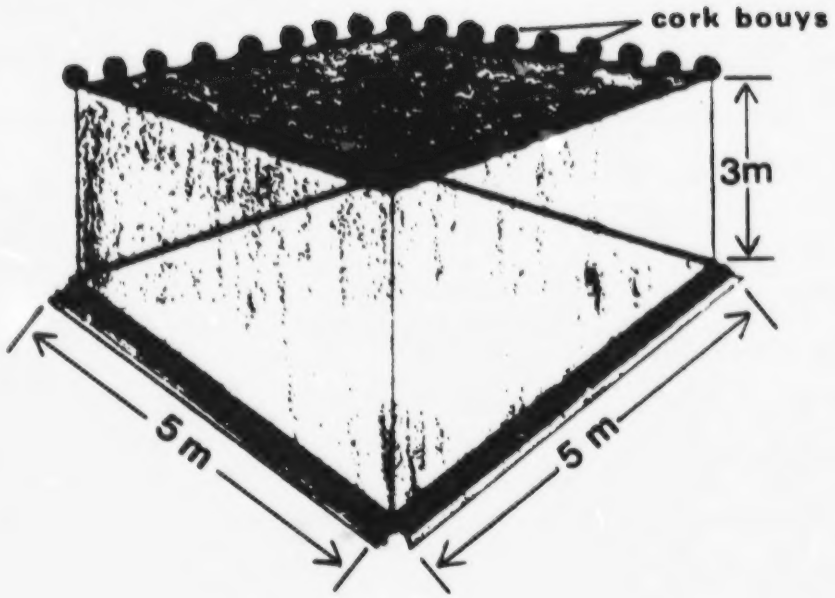
lobsters from each tray were measured to the nearest .01 g using an electric balance.

Tray tests conducted during the summer of 1982 followed the same format developed during previous years. Mud, gravel and vegetation substrates, tray densities of 25 lobsters and 4 week set periods were used. Two small fish were added to each predator treatment tray, while control trays were void of suspected predators. Sculpins, Myoxocephalus spp., were used whenever possible. Two age groups, 3 day old stage IV larvae and 6 day old stage IV animals were tested. Both age groups were subjected to various conditions of substrate and fish predation. At the end of the set period, trays were lifted and sorted and animals were analyzed using methods previously described.

Corrals

Two underwater corrals (Fig. 3) were set in the experimental area in 1980; one on mud and one on gravel-rock bottom. Both were set in approximately 6 m of water at low tide. Their dimensions were 5 m x 5 m x 3 m. The netting, which was fabricated on land, was made of fine mesh nylon sides and burlap tops. A drawstring opening, which permitted entrance by scuba divers, was situated in a top corner of each. The corrals were erected underwater. The base perimeter of each structure was secured by split, light-gauge (approx. 40 kg) train rails cut into sections 2.75 m long. Large lobster buoys were temporarily attached to the rails to facilitate their placement. The sides and tops of the corrals were floated, using small cork buoys.

Figure 3: Experimental corral. Train rails are split lengthwise through the narrow center portion, forming top and bottom sections. The sections are used to anchor the perimeter of the structure. Cork buoys float the netting above the substrate.


cork bouys
3m
5m
5 m

split
rail

Divers liberated 1400 stage IV lobsters in each corral. Observations of the settling behavior of the juveniles were made upon release. Sampling in the mud corral was undertaken using two different techniques. An air-water lift apparatus was employed to randomly collect bottom sediments in the corral. This mechanism consisted of a 1 m long 5 cm PVC pipe with an air entrance at the base and a porous collecting bag at the top. Other samples were collected by divers who entered the corral and scooped benthic mud into buckets. The mud was brought to shore and sorted, using techniques described for the mud trays.

Visual observations were periodically made by divers in the gravel corral. Rocks were overturned and small crevices were investigated. Night dives were conducted to make observations and carry out random lobster searches.

The underwater corral in 1981 was placed on a mud-rock substrate at a low tide water depth of 6 m. Approximately one thousand stage IV juvenile lobsters were introduced in mid-August. Settling behavior was observed by divers when the animals were released and periodic dives were made to clean the corral netting, record temperatures and observe lobsters.

The structure was left in Lennox Passage over winter. On November 5, 1981 eight established lobster burrows in the corral were marked by placing orange rocks (approximately 1 kg in weight) adjacent to their entrances. Monthly

dives were made to collect information on lobster activity, burrow condition, temperature and other species present.

A spring lobster collection was made on June 4, 1982. Total lengths and carapace lengths in mm of animals caught were recorded. Daytime and nighttime observations were made periodically throughout the summer. A fall lobster collection was made on September 29 and all animals captured were measured and, if possible, sexed. The structure was then lifted, terminating the corral experiment.

RESULTS

Tray Experiments

Juvenile lobsters were found in the top 7 cm layer in the mud trays. Their burrows, which were U shaped with two openings, were usually visible when seawater had drained from the beached trays. Many lobsters could be retrieved from the burrows without removing mud.

More than 50% of the lobsters found in the rock substrate were located on the bottom of the trays. Lobsters were never found stranded on the surface. The animals were usually exposed when a rock covering a solid face was lifted.

In the vegetation trays lobsters were rarely found entangled in seaweed. In this substrate the juveniles were located under rocks usually in the bottom corners, as in rock trays. In the 6-week vegetation trays a problem with decaying seaweed existed during warm water periods.

Survivorship

In 1980, 61 trays were set to test survivorship under controlled environmental conditions. No trend indicating a superior density or bottom type was observable. Repetitions often conflicted with each other yielding high survivorship on some occasions and very low values on others.

Upon sorting, it was noted that many trays contained crabs, eels or other fishes which entered between the times of filling and introducing lobsters. These 26 trays, referred to as predator treatments, had a mean survivorship of

17.6% (SE 3.6) compared with 34.5% (SE 4.0) for the 35 trays without predators (Mann-Whitney $U = 503$, $p < .01$).

In all subsequent experiments the technique of covering rock and vegetation trays immediately after filling proved successful in excluding suspected predators. Visual inspection of the mud trays by divers enabled predator removal before lobsters were introduced.

When predator-free trays in the high and low densities are grouped and identified by substrate type (Table 1), it can be observed that high mean survivorship values exist for rock and low values for mud. These findings are consistent through 2, 4 and 6 weeks. Very little change in mean survivorship is apparent on these substrates for different time periods. Survivorship in vegetation dropped off in the 6 week treatments. Badly decayed vegetation trays were omitted, however, intermediate effects were not addressed. Little difference exists between mean survivorship values for predator free density treatments grouped over substrates (Table 2).

In G-tests on predator free data from two week tray trials (Table 3), dependence of survivorship (Sur) on substrate (Sub) was not significant; however, when survivorship on rock was compared to levels obtained from mud treatments, a significant difference was observed. Analysis of predator free data from the 4-week trays (Table 4) indicated that dependence of survivorship on substrate was highly significant and each substrate type yielded significantly different survivorship levels. Data from 6-week vegetation trays were not

Table 1: Percent survivorship in predator-free lobster trays containing various substrates. $\bar{X}$ is the mean survivorship value of experimental tray units in each group.

Time (weeks)		Substrate		
		Rock	Mud	Vegetation
2	$\bar{X}$	42.3	25.0	44.0
	SE	7.6	9.9	5.0
	N	7	4	7
4	$\bar{X}$	43.6	23.6	36.0
	SE	4.8	5.2	4.8
	N	14	7	9.0
6	$\bar{X}$	40.8	22.9	26.0
	SE	6.1	7.5	14.0
	N	12	9	2
4*	$\bar{X}$	53.3	31.4	44.7
	SE	5.0	5.7	3.4
	N	19	14	17

*This 4-week group constitutes low-density trials without predators from all experimental sets.

Table 2: Percent survivorship in predator free lobster trays of low and high density. $\bar{X}$ is the mean survivorship of experimental tray units in each group.

Time (weeks)		Density	
		Low	High
2	$\bar{X}$	41.8	36.1
	SE	3.7	8.7
	N	10	8
4	$\bar{X}$	38.1	35.4
	SE	5.2	4.0
	N	14.0	16
6	$\bar{X}$	38.5	26.9
	SE	8.3	4.6
	N	11	12

Table 3: Analysis of the independence of survivorship (Sur) with respect to substrate (Sub) and density (Den) of juvenile lobsters held in experimental trays for 2 weeks. Rock (R), Mud (M) and vegetation (V) substrates are compared.

Hypothesis Tested	df	G	
Sub X Sur independence	2	5.991	ns
R vs M	1	5.304	p <.05
V vs M	1	3.840	ns
R vs V	1	0.106	ns
Den X Sur independence	1	0.930	ns
Sub X Den X Sur interaction	2	0.765	ns
Sub X Den X Sur independence	7	45.274	p <.01

Table 4: Analysis of the independence of survivorship (Sur) with respect to substrate (Sub) and density (Den) of juvenile lobsters held in experimental trays for 4 weeks. Rock (R), Mud (M) and vegetation (V) substrates are compared.

Hypothesis Tested	df	G	
Sub X Sur independence	2	9.210	p <.01
R vs M	1	50.762	p <.01
V vs M	1	20.210	p <.01
R vs V	1	6.380	p <.05
Den X Sur independence	1	0.038	ns
Sub X Den X Sur interaction	2	1.086	ns
Sub X Den X Sur independence	7	71.050	p <.01

available, however, G-tests between predator free data from 6-week rock and mud trays showed a highly significant dependence of survivorship on substrate (Table 5). Survivorship and density (Den) were found to be independent in 2, 4 and 6-week tray tests and interactions between substrate, density and survivorship were not significant.

Data from low-density, 4-week trays, which included control treatments from the predator experiments, are summarized in Table 1. These results indicate highest mean survivorship in rock, followed by vegetation, followed by mud (Kruskal-Wallis statistic = 6.60 among substrates $p < .05$). Many of the trays in this set were in the water during cool temperature periods late in the field season. All substrates in this set produced higher mean survivorship values than did the earlier (1981) experiments of 2, 4 and 6 weeks in summer.

No significant difference was observed between predator treatments (Table 6) on rock (Kruskal-Wallis statistic = 0.166) or vegetation (Kruskal-Wallis statistic = 0.491). In mud trays (Table 6) there were highly significant differences among crab, starfish and predator-free treatments (Kruskal-Wallis statistic = 11.0, $p < .01$).

Combined rock and vegetation tray data (Table 7) indicated that six-day-old stage IV lobsters tested without predators yielded highest mean survivorship values while 3-day-old stage IV fish treatment trials yielded the lowest. In G-tests on these data (Table 8) survivorship (Sur) was found to be dependent on both stage 4 age (Age) and fish

Table 5: Analysis of the independency of survivorship (Sur) with respect to substrate (Sub) and density (Den) of juvenile lobsters held in experimental trays for 6 weeks. Rock (R) and Mud (M) substrates are compared.

Hypothesis Tested	df	G	
Sub X Sur idependence	1	72.656	$p < .01$
Den X Sur independence	1	3.214	ns
Sub X Den X Sur interaction	1	0.451	ns
Sub X Den X Sur independence	4	76.342	$p < .01$

Table 6: Percent survivorship of lobsters held in trays containing various substrates and suspected predators. $\bar{X}$ is the mean survivorship of experimental tray units in each group.

Substrate		Predator		
		Absent	Starfish	Crab
rock	$\bar{X}$	55.2	54.0	60.0
	SE	7.1	8.4	3.3
	N	5	4	5
mud	$\bar{X}$	50.7	36.0	3.4
	SE	1.3	7.1	1.4
	N	3	4	7
vegetation	$\bar{X}$	48.8	41.6	48.0
	SE	6.0	3.9	10.5
	N	5	5	5

Table 7: Percent survivorship of different age stage IV lobsters held in rock and vegetation trays and subjected to fish predation or no suspected predation. $\bar{X}$ is the mean survivorship of experimental tray units in each group.

Predator	Absent		Fish	
Stage 4 Age	3 days	6 days	3 days	6 days
$\bar{X}$	51	74	43	49.6
SE	11.1	8.7	13.1	13.1
N	4	4	4	5

Table 8 : Analysis of the independence of survivorship (Sur) with respect to fish predation (Pred) and stage IV age (Age) of juvenile lobsters held in experimental rock and vegetation trays for 4 weeks.

Hypothesis Tested	df	G	
Age X Sur independence	1	7.726	$p < .01$
Pred X Sur independence	1	10.750	$p < .01$
Age X Pred X Sur interaction	1	4.828	$p < .05$
Age X Pred X Sur independence	4	24.616	$p < .01$

predation (Pred) and the interaction between stage IV age, predation and survivorship was significant. A mean percent survivorship value of 0.8% was obtained from mud trays containing fish predators.

Growth

The mean size of stage IV lobsters in each group brought to the field site was different, therefore growth measurements were based upon the percent increase from the initial length. Extreme variation in growth rates existed between lobsters held in the same experimental trays (e.g., Fig. 4). The longer the growth period, the greater the difference between largest and smallest animals. A regression analysis of the mean size increase percentage against its standard deviation for all trays showed a highly significant correlation ($p < .001$). A size-frequency distribution of all the lobsters measured in association with experimental tray testing (Fig. 5) shows no modes indicating molt stage groups.

Little difference existed among growth rates on the various substrates (Table 9). Growth rates were similar in high and low density 2-week trays, however, lobsters in low density trays showed greater growth increases after 4 and 6 week set periods (Table 10). Two-way ANOVA tests on 2-week log transformed growth data showed no significant difference between high and low densities nor among substrates. Log transformed growth data from 4-week trays showed a significant difference between densities ($F = 4.511$, $p < .05$) but no

Figure 4: Size frequency distribution of juvenile lobsters retrieved from an experimental tray which contained rock substrate and was set for 6 weeks.

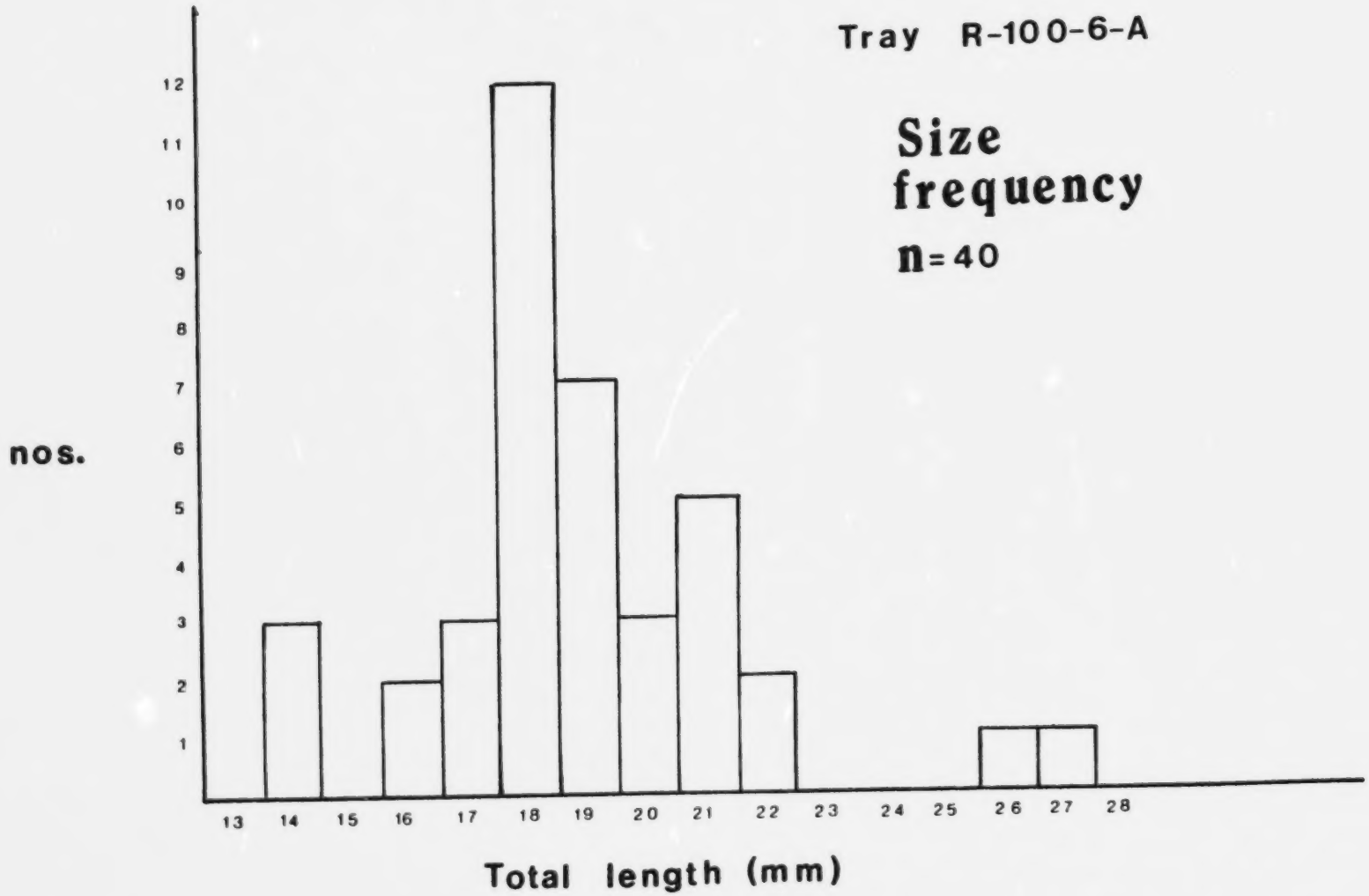

Tray R-100-6-A
Size frequency
n=40
nos.
12
11
10
9
8
7
6
5
4
3
2
1
13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28
Total length (mm)

Figure 5: Size frequency distribution of all juvenile lobsters measured in association with tray experiments.

Total sample

Size frequency

n=2432

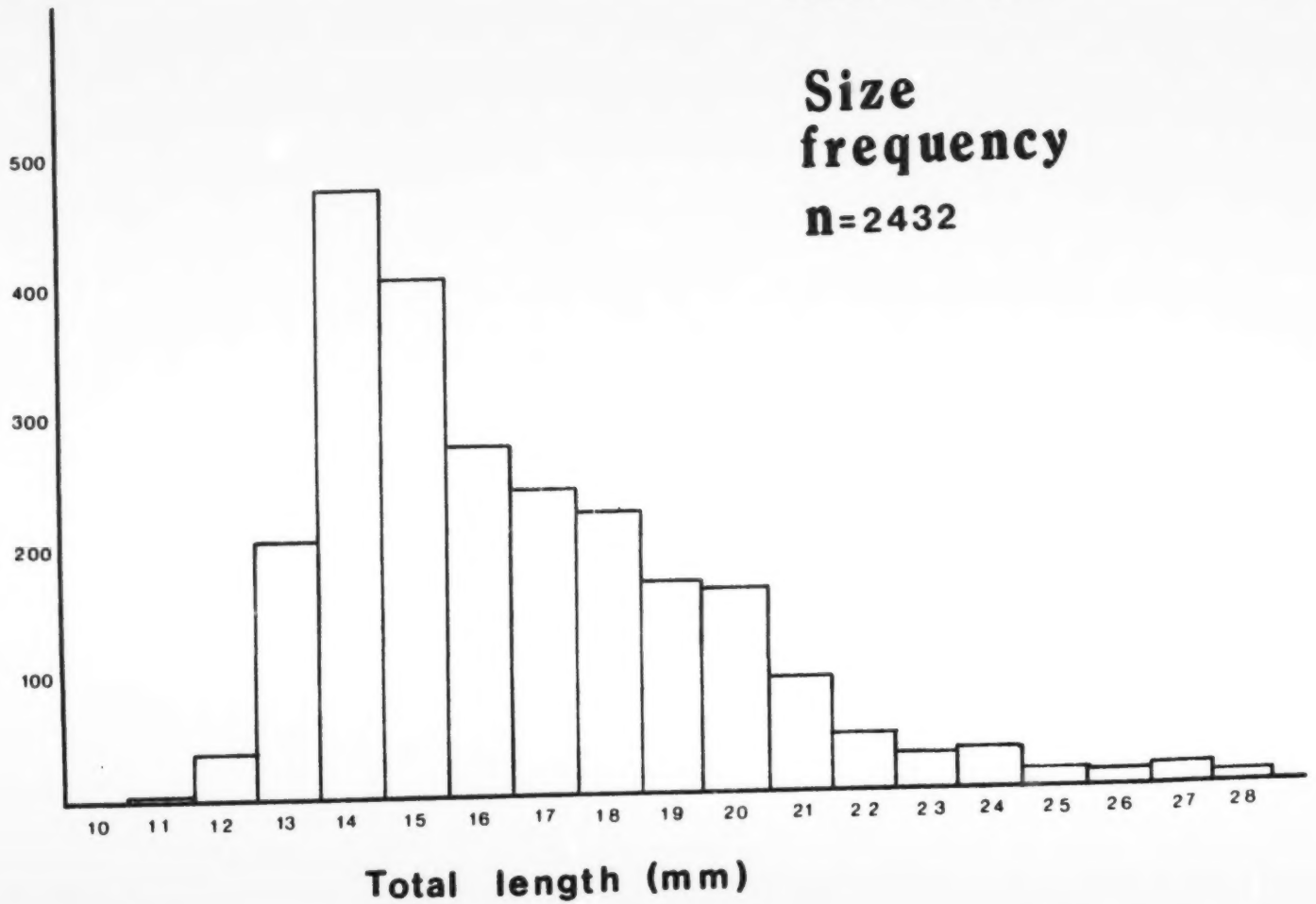


Table 9: Percent increase in total length of lobsters held in experimental trays containing various substrates. $\bar{X}$ is the mean value derived from average size increases in all trays from each group.

Time (weeks)		Substrate		
		Rock	Mud	Vegetation
2	$\bar{X}$	15.4	18.1	17.9
	SE	2.2	5.4	2.7
	N	7	4	7
4	$\bar{X}$	27.7	30.0	32.9
	SE	2.2	4.3	5.3
	N	14	7	9
6	$\bar{X}$	51.1	55.0	48.8
	SE	3.7	6.3	.9
	N	12	9	2
4*	$\bar{X}$	27.2	29.5	30.8
	SE	2.6	3.0	3.4
	N	19	13	17

*This 4-week group constitutes low density trials without predators from all experimental sets.

Table 10: Percent increase in total length of lobsters held in low and high density experimental trays. $\bar{X}$ is the mean value derived from average size increases in all trays from each group.

Time (weeks)		Density	
		Low	High
2	$\bar{X}$	17.0	16.9
	SE	1.9	3.1
	N	10	8
4	$\bar{X}$	35.4	24.8
	SE	2.9	2.5
	N	14	16
6	$\bar{X}$	59.0	46.4
	SE	4.6	3.4
	N	11	12

significant difference among substrates. The interaction between substrate and density was not significant for either of the 2 and 4 week data sets. An empty cell prevented a 2-way ANOVA on data from 6-week trays. Comparisons of log transformed 6-week growth data grouped over substrates showed a significant difference ($F = 5.08$, $p < .05$) between densities. No significant difference in growth was found among substrates in tests on this data grouped over high and low densities.

Corral Experiments

All work inside the mud corral was severely restricted due to lack of visibility. Any movement by divers would stir up the bottom sediment making observations impossible. No information could be acquired on settling behavior in this substrate and no accurate visual inspections of the bottom could be made during the course of the testing. Several attempts were made to retrieve juvenile lobsters using an air water lift apparatus. This mechanism proved successful in gathering sediments, however, no lobsters were found within. A number of mud samples taken from the bottom of the corral were carefully washed and sorted, but this technique also proved unsuccessful in finding the juveniles. Sampling efforts in the mud corral ceased after several weeks and the structure was removed from the bottom.

Visibility was not a severe problem in the 1980 corral placed on mixed rock, gravel and mud substrate. Upon release, the lobsters either swam upward toward the roof of

the corral or slowly drifted downward until they reached the substrate. When on the bottom, the lobsters walked slowly about and after a brief period either began burrowing or left the substrate to resume swimming. Some of the swimmers that remained in view were observed settling to again make contact with the bottom. The fate of those lobsters swimming to the roof of the corral is unknown.

The juvenile lobsters burrowed by orienting their claws under a rock or other solid object, disturbing the sediment with their walking legs, and fanning rapidly with their pleopods. These activities dislodged and washed away fine sediments to create a depression under the object. During construction procedures, the lobsters occasionally turned to face outward and moved in and out of their burrows. If a suitable crack or crevice was available, juveniles often entered and were out of sight before any burrowing behavior was observed. After a period of 15 to 20 minutes, no lobsters were visible on the substrate surface.

A number of the released juveniles were immediately eaten by small eels or other fishes. These predators rested motionless on the bottom, quickly approached and then swallowed the lobsters as they settled towards the substrate. Lobsters were not observed actively avoiding or escaping an attack.

Lobsters were not found by divers who made a number of day and night searches in the corral within 21 days after the introduction of the animals. Several weeks after stocking, inspection of the corral bottom revealed small openings

in sediments adjacent to rocks. Lobsters could then be dislodged by probing the substrate, exploring the holes and overturning the rocks. This digging, however, stirred up the sediment, making visibility poor and capture of the juveniles difficult.

In 1981 the experimental corral was placed on a substrate or rock, gravel and mud comparable to that of the 1980 rock corral. The settling and burrowing behavior of the animals released in the structure was similar to that previously described. Again fish and eel predators were observed taking lobsters.

Several weeks after the lobsters were introduced, burrow openings, which were usually associated with a solid object, were clearly definable. Juvenile lobsters were not found out of their burrows at any time when day and night summer observations were made. When marker rocks were put in place in the fall, some burrows were quite large and lobsters could be seen moving within. Burrow sharing was never observed.

The activity of the juvenile lobsters in the corral changed with changing temperatures. On December 8 the bottom temperature was 6.5^{o}C, burrows were present and well maintained and lobsters were seen moving inside. Orange marker rocks were still adjacent to burrow entrances and in some cases were used as part of the burrow structure. One dislodged lobster estimated at 30-40 mm total length was very active and escaped capture.

On January 12, 1982, the bottom temperature was 0.5^{o}C,

burrows were open and found adjacent to orange rocks, but they did not appear well maintained. No lobster activity was seen. One juvenile approximately 20 mm (total length) which was removed from its burrow was inactive, showing only slight beating of its pleopods.

In February ice moved the corral marker and a bottom search could not find the structure, therefore observations could not be made. The bottom temperature recorded during the search was -1°C. On March 19 the corral was found intact and the marker was put back in place. Remnants of burrows were found adjacent to some orange rocks, but they were not well maintained and no lobster movement was seen. One unmarked burrow was investigated, but no lobster was retrieved. The bottom temperature at the time of this dive was -1°C.

On April 21 the bottom temperature measured in the corral was 1.5°C. The remnants of some lobster burrows were apparent, but they did not seem to be in active use. No lobster activity of any sort was observed.

On May 13, the bottom temperature inside the corral was 5°C. Burrows were present and well maintained and lobsters could be seen moving within. At 3 orange-rock sites burrows were observable, but none were found at 2 other marked locations. One very active lobster estimated at 40 mm total length was chased out of an unmarked burrow, but could not be captured.

The bottom temperature recorded at the time of the June 4 lobster collection was 9°C. Inhabited burrows were

present next to 5 orange rocks and an additional 2 marked sites had no structures associated with them. Burrows were probed and destroyed in attempts to collect the lobsters. Six animals were caught from approximately 12 that were dug out (Table 11). A number of burrows were observed under the rail surrounding the corral. The entrances to these burrows were on the inside of the structure and the resident lobsters appeared quite large. No attempts were made to retrieve these animals.

No juvenile lobsters were seen outside of burrows during night observations made in the corral throughout the summer. In September it was noted that the lobsters which were housed under the rails spent time at the entrances of their burrows and would respond aggressively with claws spread when they were disturbed. Continued assaults would result in their retreat out of sight. Examination of the outside of the corral revealed entrances to these burrows on the exterior.

During the fall collection of lobsters a total of 11 animals was taken, showing even greater size variation than did those taken in spring (Table 11).

Table 11: Size (total length in mm) of lobsters retrieved from the experimental corral on June 4 and September 29, 1982.

Size (total length mm)	Spring Sample	Fall Sample	Sex
23	2		
25	1		
26	1		
34		1	
35	1		
39		1	
42	1		
53		1	
58		1	
60		1	
63		1	
65		2	Male, female
73		1	Female
78		1	Female
81		1	Male

DISCUSSION

Tray tests have shown that under the conditions established for these experiments a rock substrate will enable highest survivorship for juvenile lobsters. The many cracks and crevices on this bottom type allow young settling larvae to quickly get out of sight and into the dark shelters of the interstitial spaces. Although no prior information is available on juvenile survivorship on various substrates, results from preference tests are consistent with these findings. Botero (1980) found that in the lab stage IV lobsters preferred a substrate of rock with overlying patches of seaweed over mud, gravel or sand. She also noted that lobsters were not found entangled in the plants, but instead below rock, as was observed in the vegetation trays. The U-shaped tunnels found in the mud substrate were similar to those described by Berrill and Stewart (1973)

The longest duration of a tray experiment was 6 weeks. The lobsters at the end of this period were still very small, the largest encountered being 28 mm in total length. With animals of this size, density did not appear to effect survivorship. With large lobsters crowding in the trays could have been a problem.

When settling to the ocean bottom, larval lobsters become accessible prey for various benthic invertebrates and demersal fish. In mud trays both fish and crabs had extreme effects on lobster survivorship. It is suspected that these

predators captured the lobsters before or during burrow construction. Observations in the corral indicated that fish could easily take small lobsters that were settling in their vicinity. Although survivorship on rock and vegetation substrates was lower when fish were present, most lobsters were able to get under cover before heavy predation occurred. The juveniles on these substrates would not be accessible to crabs once they were below the surface and tray tests indicate that they were not captured during settling procedures. In general, it can be assumed that the quicker a larval lobster takes cover when it reaches the bottom, the greater will be its chance for survival. Botero (1980) in lab experiments found that settling time was quickest on rock substrate, lending support to the findings of our predator tests.

Starfish did not have a significant effect on lobster survivorship on any substrate. They were a suspected predator because on two occasions in 1980 during tray sorting procedures, they were found ingesting juvenile lobsters. It was not known whether the lobsters were alive or dead when they were taken by these starfish.

The tremendous variation in growth rates between lobsters held under similar conditions in each experimental tray is not a newly found phenomenon. Hedgecock et al. (1976) with lab studies found that families raised simultaneously under optimal conditions of temperature and diet grew at significantly different rates. He noted that growth may not be predictable on the basis of genetic stock alone. This

is consistent with findings from our research, in that all the lobsters in each tray were hatched from the same female. Nelson and Hedgecock (1977), in doing electrophoretic screening of proteins from the eggs and larvae from wild caught female lobsters, found evidence of multiple parentage. This occurrence, however, was rare as previous examination of over 30 progenies revealed only Mendelian ratios.

Stewart (1968) noted that restricted conditions which forced a high degree of association between lobsters resulted in greatly reduced molting frequencies in adult males. Cobb (1970) found that when paired stage IV lobsters were held in small freezer containers in a lab, delays in molting to stage V were shown by one member of each pair, and Cobb and Tamm (1974) reported that when held in pairs, stage V and XI juveniles prolong the time between molts an average of 25-30%. Slower growth rates in high-density trays were possibly due to a greater degree of such association between the juvenile lobsters. Decreased food availability per lobster may also be a factor in these treatments. Aiken (1980) reports that nutrition can effect the growth rates in Homarus. Botero (1980) noted that growth of juveniles was faster on mud than on rock, but no significant difference among substrates was found in the present study. No assessment of the available food organisms was made for the different substrates in the trays, but it is suspected that food abundance is partially responsible for growth differences among trays.

Aiken (1980) has reported that various environmental

conditions can affect the increment of increase at molting as well as the intermolt period. Differences in percent size increase for lobsters of a similar size may be a natural occurence, as in this study distinct molt groups were not distinguishable, and no evidence of predictable size increases from stage IV onward was apparent.

The visibility problems in the mud corral made observations impossible. The sampling techniques employed were not effective in catching lobsters. It is not known, however, whether the juveniles were present and able to escape collection or simply not successful in establishing burrows. Some fish and crabs found in the mud corral could have preyed upon many of the settling larvae.

The settling behavior observed in the corral placed on rocky substrate was similar to that described by other researchers. Botero (1980) described a pattern of touching down and walking about, followed by either burrowing or swimming. She suggests that when stage IV larvae make contact with the substrate they get various thigmotactic cues which will influence their bottom selection. Some lobsters, when released in the corral, swam up toward the roof of the structure. These individuals were presumably still photopositive and not advanced enough in stage IV to seek cover on the bottom. Ennis (1975b) noted that early, 0-2 day stage IV larvae moved to the surface when released at the bottom, while late, 14-15 day stage IV lobsters remained at the bottom.

Initially, it was very difficult to find the juvenile lobsters inside the rock corral. This situation paralleled results in the wild where countless hours of diving uncovered no stage IV, V or VI juveniles. Stage IV larvae are very effective in getting out of sight and burrow well below the substrate. The coloration of the young juveniles enables them to blend with environment, and even when dislodged they can be difficult to locate. The burrows of the very small lobsters in the corral were obscure and not quickly recognizable to an untrained eye. It would take an experienced diver to identify them and flush out juveniles inside.

As the lobsters grew, their burrows within the corral were easily identifiable. In most cases the structures were constructed next to solid objects which were used as roofs. Howard and Bennett (1979) found that in the laboratory European lobsters placed on soft substrate preferred to burrow against a solid surface. Pottle and Elner (1982) noted that stage VII-X juveniles held in the lab constructed burrows in silt clay that were invariably adjacent to supporting structures. Cooper and Uzmann (1977) collected a number of stage IV to X lobsters from mud substrate in the wild and noted that nearly all individuals were retrieved from tiny burrows excavated next to solid objects.

Juvenile lobsters were not seen outside of their burrows at any time, suggesting that they spend their entire early existence within their burrows or tunnel systems. Herrick (1911) reported that young lobsters are out of sight

and undercover until a size of approximately 90 mm total length, at which time they begin to explore the ocean bottom with more boldness. Cooper and Uzmann (1977) found that juveniles less than 40 mm carapace length (approximately 100 mm total length) spent their entire time inside their burrows. They noted that at 35-40 mm carapace length they become partially active at night, moving back and forth within the entrance of their shelter and occasionally outside. Some of larger animals observed under the rails of the corral were displaying this type of restless behavior when observed during night dives.

At some point the behavior of juvenile lobsters shifts and they commence their nocturnal rhythm of actively foraging on the ocean bottom. Lang et al. (1977), in studying lobster behavior, found that in larvae and early juvenile stages, morphological and physiological factors favored escape over defense behavior. As lobsters grow and their body proportions change (relative length of the abdomen and cephalothorax), the escape response is replaced by a defense behavior.

Shelter sharing does not appear to be a normal occurrence in the wild. Cooper and Uzmann (1977), during field studies, found no shelter sharing by animals of the same size range, supporting observations made in the corral. O'Neil and Cobb (1979) in the lab found that lobsters of the same sex and carapace length would share shelters if the animals were missing one or both claws.

It is not known whether the same lobsters occupied

the same burrows throughout the course of the burrow marking experiment in the corral. It was observed that the identified burrows were in constant use from the time they were marked in November until lobster activity ceased when the water cooled. Based upon the observed behavior of the juvenile lobsters, it is unlikely that the animals would move over the corral substrate and interchange burrows. It is suspected that the burrows, once established, would remain in the same location for an extended period of time and the resident lobster would not change.

The overwintering experiment in the corral indicated that the resident lobsters of the marked burrows remained in their shelter and inactive during the cold water months. With warming temperatures, their activity increased and their burrows were once again well maintained. Thomas (1968), while studying large juvenile lobsters in the Bideford River Estuary in Prince Edward Island, found that they constructed mud burrows in the fall and remained in them inactive and docile during the colder water months.

Consistent with tray results, growth rates in the corral were extremely variable. Samples taken in the spring displayed large differences in size after only one growing season. The fall samples of animals nearing completion of their second growing season showed even greater variation. Taylor and Baird (1947) obtained similar results in lobster planting experiment in Schoodic, Maine. They planted stage IV lobsters in a small cove in early summer and retrieved

them when the cove was drained in mid-November. The 22 lobsters which were found burrowed beneath rocks just below the low tide mark ranged in size from 25 to 53 mm in total length with a mean of 44 mm. Hughes and Matthiessen (1962) also report on this issue, noting that considerable variation in growth rates existed among individual lobsters held for 10 years.

The reasons for the variations in growth rates are many. Temperature has a major effect, but when constant, other factors, including environmental conditions and genetic variability, combined with physiological and behavioral patterns will have an influence. It is suspected that substantial variation in growth rates is a natural phenomenon. It is possible to produce growth equations and to estimate size at age, but it should be expected that large deviations from the predicted means will exist.

In assessing lobster populations, the inability to determine age and growth rates makes the prediction of year class strength difficult. In addition, the problem in finding young juveniles makes quantitative assessment of small size groups impossible. At the present time, the only reliable indication of the strength of a future fishable lobster population will come from information on trapable pre-fishery recruit lobsters. Due to variations in growth rates, two-year or three-year pulses in landings may actually be the result of one strong year class moving through. If larval settling success and the time range to legal size could be assessed, it may then be possible to estimate when good or

lean years for lobster fishing will occur. More study on these issues is needed before these goals can be achieved.

These tests have shown that hatchery-reared animals can be successful in the field. They survived to some extent on all the substrates that were tested. These results are supported by Howard and Bennett (1979), who noted that juvenile lobsters have wide substrate tolerances. In tray experiments wide variation in survivorship existed on all bottom types. These variations were due to factors such as fitness of the animals or unknown environmental influences which could not be controlled. In general, a substrate which provides ready shelters, enabling the larvae to get out of sight and danger, will produce highest survivorship. How a stage IV lobster larva could orientate itself to such substrates in the field is unknown.

In our tests and others described in the literature, rock substrate appears superior with presence of macrophytes adding no significant further advantage. Possibly a dense seaweed cover could impede the movement of larvae to the bottom exposing them to additional predation before burrows are found. On the other hand, macrophytes could conceal settling larvae, allowing them to find a burrow before a fish predator finds them. These two effects may tend to cancel out.

More information is needed on the age at which stage IV larvae are prepared to settle to the ocean bottom and the time of day at which this transition occurs. With such additional knowledge, the present understanding of

suitable substrates and the hatchery techniques that are currently employed, the possibility of stocking depleted lobster grounds with artificially reared stage IV animals may become a reality.

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